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Chronicles of *Darna pallivitta* (Moore 1877) (Lepidoptera: Limacodidae): biology and larval morphology of a new pest in Hawaii

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Abstract. The biology of *Darna pallivitta* (Moore 1877), an Asian species of nettle caterpillar recently introduced to the island of Hawaii, is described from this island population. The species is highly polyphagous and has stinging caterpillars commonly associated with Limacodidae. Information on mating, oviposition, potential fecundity, duration and number of instars, cocooning, pupation, and total development time are included. The female at eclosion was found to have 573.5 ± 184.1 eggs, of which 201.5 ± 53.5 were mature. Similar to other spiny species of Limacodidae, *D. pallivitta* was found to not feed until second instar. The duration of immature stages were as follows: egg (7.0 d), larval (53.0 ± 6.9 d), and cocoon (19.1 ± 1.0 d). First and second instars are described for the first time for a *Darna* species. In a family known for heteromorphic larvae, this is the first known example of a limacodid species with elongate first instar tubercles, which later develop into spiny, urticating scoli rather than becoming smooth bodied or retaining tubercles that become hairy. Caterpillars from 6th instar or later have a delayed phenotypic expression of SD2 verrucae closely associated with spiracles on A2 to A7. Larval stages varied from 8–11 instars with a total larval duration of 45–72 d. Eleven instars equal the maximum reported for Limacodidae. Pupation took place on the fifth day after cocooning, which is a brief period compared to other members of the family. The total time from egg hatch to adult eclosion was 80.0 ± 7.1 d. Adult life span was found to be 11.0 ± 1.3 d in females and 9.7 ± 1.1 d in males.

Key Words. Lepidoptera, Limacodidae, *Darna pallivitta*, number of instars, fecundity, larval morphology, invasive species to Hawaii.

INTRODUCTION

The nettle caterpillar, *Darna pallivitta* (Moore 1877), is a new immigrant pest to Hawaii that was first noticed in September 2001 after workers at a nursery on the island of Hawaii were being "stung" by a caterpillar while handling rhapis palms (*Rhapis* sp.)(Conant et al. 2001). It was suspected of having entered the state on potted palm plants legally imported from Taiwan. Immediately after its detection, an eradication attempt with pesticides was made but proved unsuccessful. In January 2002, surveys showed its establishment on three surrounding farms where the larvae were found feeding on coconut palm (*Cocos nucifera* L.), areca palm (*Chrysalidocarpus lutescens* Wendl.), rhapis palm, Hawaiian ti (*Cordyline terminalis* Kunth), and *Dracaena* sp.

Darna pallivitta is now well established on the east side of the Big Island (island of Hawaii) and has slowly moved from the original infestation site southward during 2004 and 2005. The polyphagous habit of *D. pallivitta* increases its pest potential in Hawaii. Field observations of feeding damage include both weedy and ornamental plants commonly grown in residences and agriculture. Damage to ornamental plants could result in economic losses to the nursery industry. Also potentially threatened

by larval feeding are endemic plants and palm species, including the ubiquitous coconut palm. Of medical importance are the stinging spines of the larva, which cause dermatitis on contact with the skin. Reports of humans being "stung" by *D. pallivitta* larvae increased during an outbreak in a residential community during 2005 (P. Conant, personal communication). The combination of stately trees such as the coconut palm becoming unsightly or removed due to defoliation and the annoyance by medical problems from caterpillar spines has a potentially damaging impact on Hawaii's visitor industry.

Marc E. Epstein (at the time with the Smithsonian Institution, Washington D.C.) and Cheng-shing Lin (National Museum of Natural History, Taiwan) identified the original Hawaiian specimens of *D. pallivitta*. According to Holloway et al. (1987), *D. pallivitta* occurs in China, Taiwan, Thailand, western Malaysia, Indonesia, and Java, and its host plants in those regions include *Adenostemma* sp., *Areca* sp., *Breynia* sp., coconut, *Ficus* sp., grasses, maize, and oil palm. It is considered only a minor pest of coconut palms in its natural range, probably due to the presence of natural enemies that do not occur in Hawaii. Chayopas (1982) (unpublished and from Holloway et al. 1987) presented the following life-history data of *D. pallivitta* from Thailand for the mean duration of developmental stages (and their ranges): egg 4.8 d (4–5), larva 40.1 d (40–53), pupa 13.3 d (11–15), which likely represents the entire cocoon period as discussed further on, and adult 5.3 d (3–7) [note: the larval mean duration appears to be miscalculated, as it is too low based on the given range].

Given the potential for the spread of this species in Hawaii and beyond, we undertook a study to provide basic knowledge of the biology of *D. pallivitta* in the hope that it will aid in the development of monitoring and integrated control strategies. Previously there has been no detailed information on the biology, including life history and larval morphology, of this species in the literature other than the aforementioned unpublished information by Chayopas. We provide a description of the life history of *D. pallivitta*, which includes an unexpected morphological and developmental find: the first known example of SD2 verrucae in spiny limacodid caterpillars, which is not phenotypically expressed until later instars. Furthermore, *D. pallivitta* is presently the only limacodid caterpillar known to develop spiny scoli or verrucae from elongate tubercles found on the first instar; in subsequent instars these tubercles are normally transformed into simple hairlike setae or remain, becoming hairy rather than spiny (Epstein 1996).

Materials and Methods

Biological studies of *D. pallivitta* were conducted at the Hawaii Department of Agriculture (HDOA) Quarantine Laboratory in Honolulu (Oahu Island) during 2002. A colony was established from 26 cocoons received from the HDOA Hilo Insectary (Big Island) during March 2002. Cocoons were placed in a cage (42 × 42 × 62 cm) with Lumite™ screen (amber, 52 × 52 mesh, SI Corporation, Gainesville, GA) for emerging adults to mate and oviposit. Leaf bouquets of three plant species, coconut palm (*Cocos nucifera* L.), areca palm (*Chrysalidocarpus lutescens* Wendl.), and Hawaiian ti (*Cordyline terminalis* (L.)), were initially offered to larvae for feeding; however, only *C. terminalis* was ultimately used for maintaining the laboratory colony due to its larger leaf size and greater availability. Rearing conditions for all studies were 24.6 ± 1.5°C, 70.6 ± 5.2% RH, and 12:12 (L:D) photoperiod.

The life cycle was determined by observing 25 larvae, each isolated in a disposable petri dish (100 × 15 mm) lined with a #1 filter paper (9 cm round). These were reared individually and monitored almost daily to determine the number of instars. A petri dish was emptied of frass each time a larva was checked. Each new instar was determined by the presence of a molted skin, but in some cases, a molted skin was not found because the larva ate it. If this occurred, molting was based on two observations: the color change in the larva from dark to light and the absence of frass, which indicated that no feeding took place the day before molting. Due to their retractile heads (Epstein 1996) and feeding on cast skin, head capsules of the various larval instars could not be accurately measured. Larvae were fed the leaflets of areca palm throughout the study. A leaflet about 15–20 cm long was wrapped with a wet 1 cm wide strip of cotton at about 2 cm from its base and then snugly plugged into a small water-filled 1-dram glass shell vial (9 mm outer dimension × 30 mm length). This "bouquet" was placed in the petri dish so that the leaflet curled around the inside and was replaced when it began drying out (about 3 days) or was consumed. Precaution was necessary to avoid the stinging spines of the larva beyond the first few instars (Figs. 4 and 6).

All measurements for eggs, cocoons, and adult forewing length (= tegula to wing apex) were done under a Wild M8 dissecting microscope fitted with an ocular micrometer (0.02 mm units) at 25× or 50× magnification. Measured eggs were obtained from the laboratory colony deposited on *C. terminalis* leaves. Age of pupation within the cocoon was determined by cutting an oval, lengthwise observation window on one side of the shell (Fig. 21). A water-soluble glue (Lepage's, Gloucester, MA) used for pinning insects was carefully dabbed around the edges of the opening with a brush, followed by firm placement of a #2 glass cover slip (15 mm round) to complete the seal. In previous dissections of cocoons of known ages, pupation was found to occur at least 5 days following construction; therefore, windows were made when the cocoons were 3 days old. A total of 12 cocoons, three each that cocooned on 4 successive days, were "windowed" for observation and then checked daily for pupation.

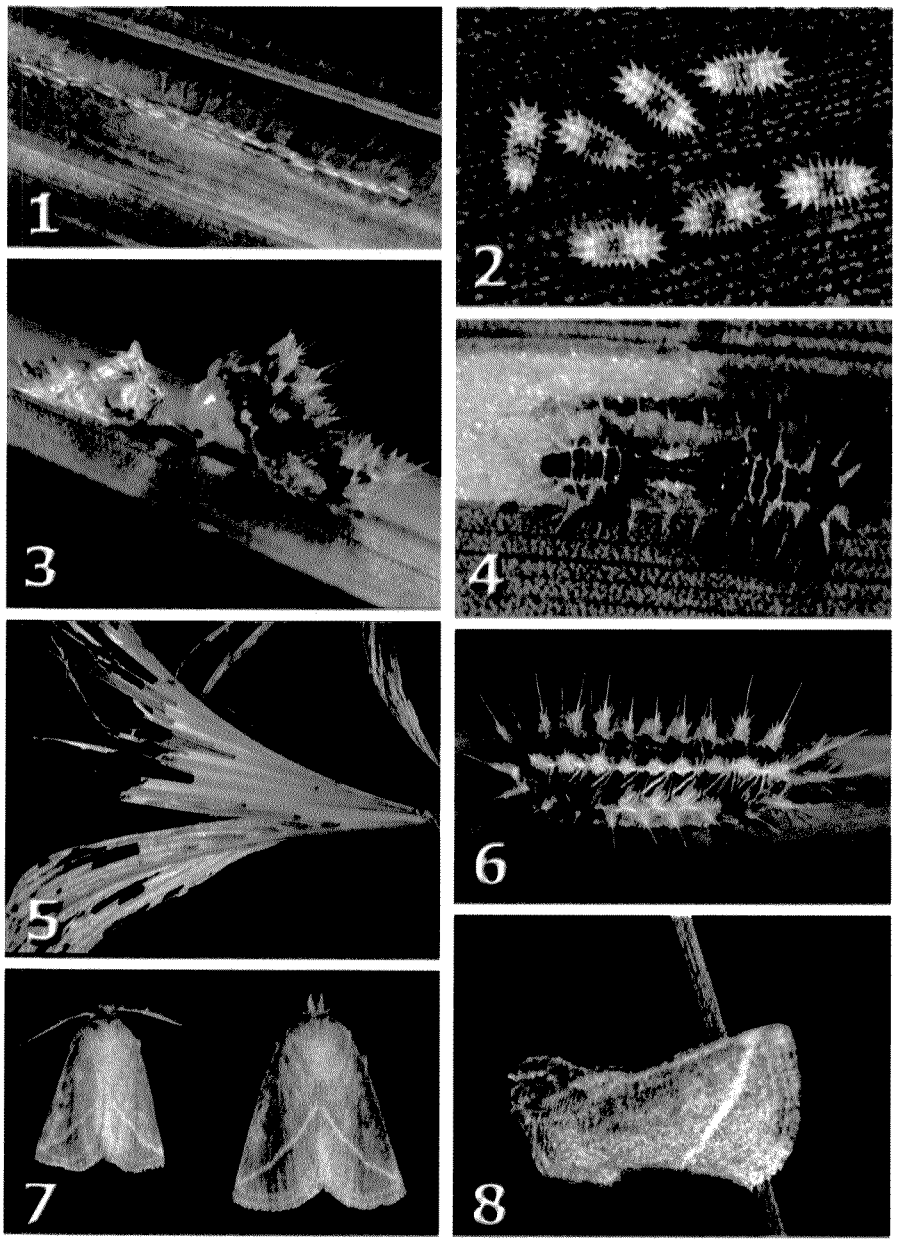
Mating and fecundity studies were conducted by pairing a one-day old female and a male adult in a wide-mouth glass gallon jar with an organdy cloth cover secured by rubber bands. Although intake of fluids is reported for adult Limacodidae (Epstein 1996), individuals were not given liquid prior to mating or oviposition. The entire jar was placed horizontally on a wooden rack. Each day, the adult pair was transferred to a new jar. Ten pairs were monitored daily for oviposition and longevity. The number of eggs deposited in the jar of the previous day was counted from the outside of the glass. As larvae hatched, they were removed from the jar with a fine-tipped brush and counted. This procedure was repeated until hatching ceased.

Counts of ovarian eggs to determine potential fecundity were done by dissecting ten one-day old females and removing their ovaries. The ovaries were placed in a glass petri dish (100 × 15 mm) with water and then the ovarioles "untangled" with a teasing needle. Counts of mature and immature eggs were done for each ovariole under a Wild M8 dissecting microscope. Eggs at the basal end of the ovariole, closest to the common oviduct, were considered to be mature, whereas others that showed a subtle change to a smaller size in the direction of the distal end of the ovariole were deemed immature.

RESULTS

Life Stages. Egg: Females mostly deposited the flat, scalelike eggs in masses, sometimes in a long line (Fig. 1), or singly. In the laboratory, females laid eggs on the cage interior and on the bouquets of host leaves. Egg masses were typically the width and length of two or three eggs with successive eggs overlapping; they appear as a translucent sheen on the leaf surface that is easily overlooked, blending in with the leaf color. Each egg is elliptical and measures about 1.1 × 1.6 mm (Table 3). Newly deposited eggs are yellow and within several days the embryo can be seen within as it develops. Duration of the egg stage was 7 days (Table 1).

Larva: All instars of *D. pallivitta* have the basic limacodid form with retractile head, small thoracic legs (Fig. 14), smooth elastic cuticle and sucker disks on the ventrum without crochets (Figs. 9–10), and an anal proleg with shagreened cuticle (Fig. 18) (Epstein 1996). The 1st instar is a nonfeeding stage that lasts two days (Figs. 2 and 9); it is pale yellow with a darker red-brown center and is gregarious (Fig. 2) in the sense that it hatches from clusters of eggs. The head has a fishtail-shaped spinneret, which is found most limacodids, particularly in the 1st instar, and in dalcerids (Epstein 1996); this shape is maintained throughout all instars (Figs. 11–12). The labrum has comblike spinules along the anterior margin (Fig. 11). The prothorax has two hairlike L (= lateral) setae anteroventral to the spiracle, while the other primary setae throughout this segment are of the same type, characteristic of limacodid caterpillars in all instars (Fig. 9)(Epstein 1996). The meso- and metathoracic segments (= T2 & T3) and abdominal segments A2 to A8 have two pairs of elongate tubercles on each segment, which correspond to one D (= dorsal) and SD (= subdorsal) seta on each side; these appear to be nonurticating and are branched at the apex (Fig. 9). Tubercles in limacodids are fleshy setae normally found only on 1st instars and are either simple or once divided at the apex (see discussion further on and Epstein 1996 for the homologies of these tubercles). On segment A1 the SD tubercle is missing and has a spiracle in its place, which is situated more dorsad than the line of spiracles to the posterior (Fig. 9). This condition is typical of known spiny limacodid caterpillars and persists throughout all instars. On A9 there is only one tubercle on each side; similar examples in other spiny caterpillars were considered to be a D tubercle by Dyar (1899), however it probably represents a fusion and reduction of D and SD tubercles (note: D and SD tubercles were referred to as subdorsal and lateral by Dyar 1899). The L setae of T2 and T3 and the abdomen have a hairlike dorsal member and a reduced, fungiform ventral member. *Darna pallivitta* is typical of limacodid species with spiny caterpillars in having a large increase in the number of spines, particularly between the 1st and 2nd instars (compare Figs. 9 and 10). The 2nd instar (Fig. 10) is the first feeding stage. Tubercles from the previous instar are transformed into spiny scoli, each with a broad and more elongate central spine that appears to be urticating. These scoli are surrounded by five or more spines on the D row and have four that are urticating and one that is a tactile seta along the bottom on the SD row. The more ventral of the two L setae on T2, T3 and the abdomen becomes hairlike rather than fungiform, as in the 1st instar, although it is shorter than its dorsal counterpart. Another change that occurs with the 2nd instar is the appearance of skin spines throughout the lateral and dorsal surfaces; these become capitate in later instars (Fig. 16). In subsequent instars the spines on the scoli increase in number while the caterpillars develop a variegated pattern of black patches and lighter orange brown in contrast to the



Figures 1–8. Life history and biology of *Darna pallivitta* (photographs by W. Nagamine). Fig. 1. Eggs. Fig. 2. First instars soon after hatching. Fig. 3. Newly molted 3rd instar and cast skin (note: head is fully exposed). Fig. 4. Fifth instar feeding on one leaf surface. Fig. 5. Early instar feeding damage on coconut leaf from early instars above and late instars below. Fig. 6. Stinging late-instar. Fig. 7. Adult male (L) and female (R). Fig. 8. Live adult resting posture (ventrum above).

light yellow or sometimes pink scoli (Fig. 6). The dark patterning does not extend below the SD scoli on A3 to A6; it produces a dumbbell appearance when viewed laterally or dorsally (Figs. 3–4). By the 6th instar the scoli are noticeably more elongate and nearly equal in size on T2, T3, A1, A2, A7 and A8 of the D row, the A9

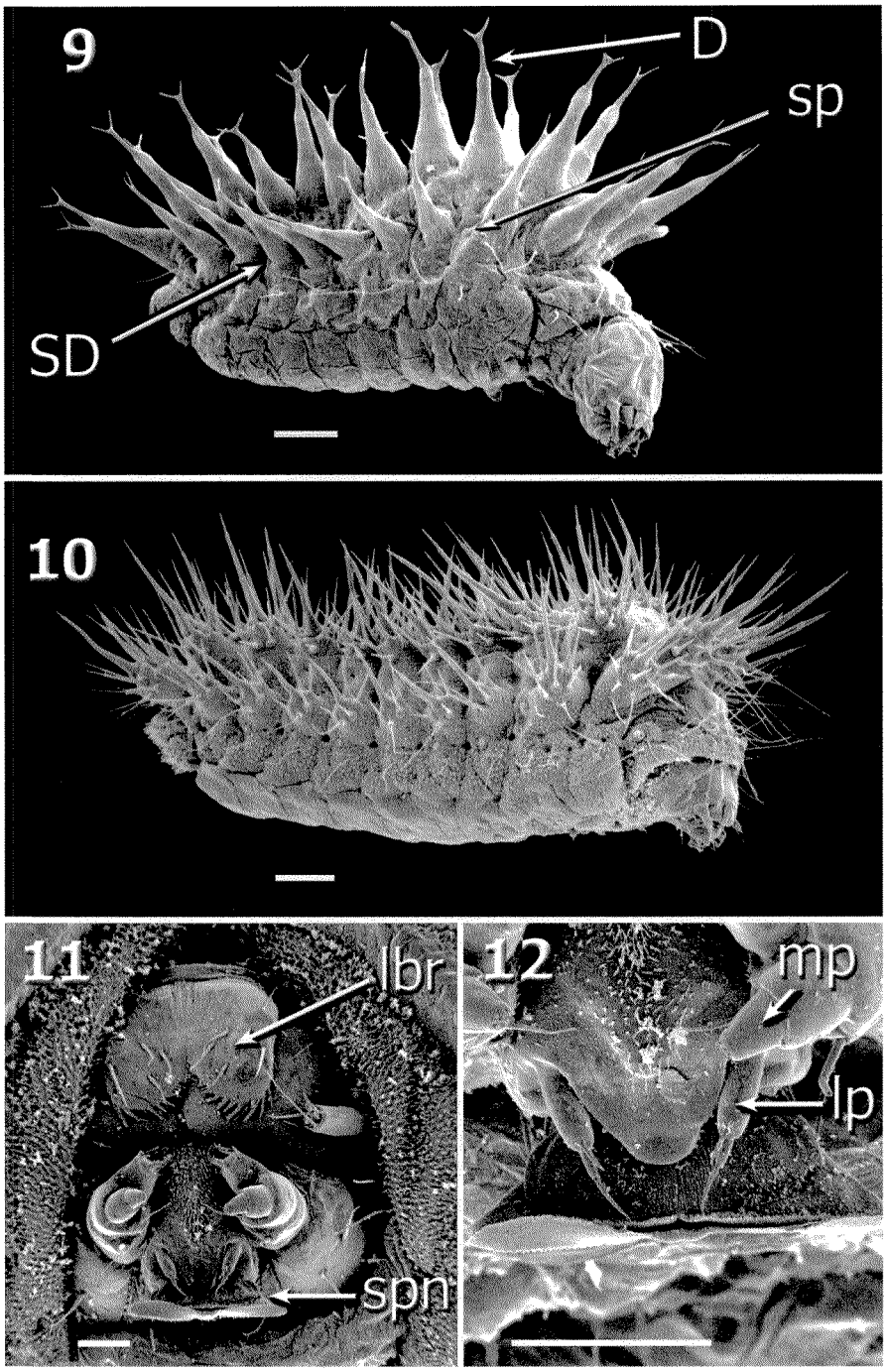
Table 1. Duration of developmental stages of *Darna pallivitta* reared individually on excised leaflets of areca palm.

Stage	N	Mean ± SEM (days)	Range (minimum to maximum days)
Egg	25	7.0 ± 0	7
Larva			
Instar 1	25	2.0 ± 0	2
Instar 2	25	5.8 ± 0.8	5–7
Instar 3	25	6.3 ± 0.5	6–7
Instar 4	25	6.0 ± 0.7	5–7
Instar 5	25	6.0 ± 0.6	6–8
Instar 6	25	6.9 ± 0.3	6–7
Instar 7	25	7.2 ± 0.9	6–9
Instar 8	25	8.2 ± 1.0	7–11
Instar 9	13	8.5 ± 1.3	7–11
Instar 10	5	8.2 ± 1.1	7–9
Instar 11	1	9.0	9
All larval instars	25	53.0 ± 6.9	45–72
Pupa	12	5.0 ± 0	5
Cocoon	25	19.1 ± 1.0	17–21
All stages	25	80.0 ± 7.1	72–99

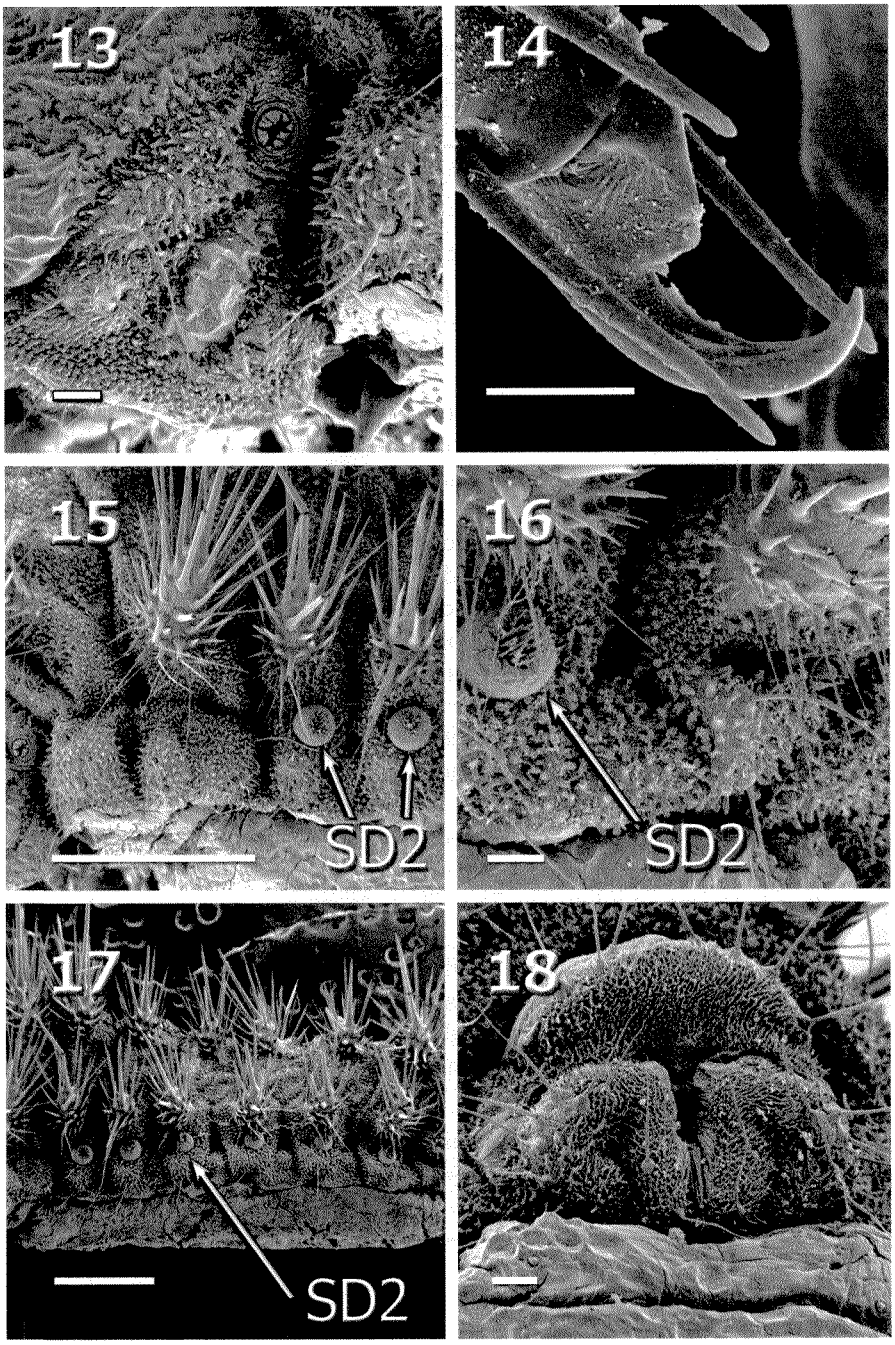
scolus, and on all segments of the SD row except on A1, where they are absent; those on the D row of A3 to A6 are short compared to all others (Fig. 6). All of these scoli develop dark spines except for the more elongate, pale colored central spine, which is always slightly longer than the scolus that bears it. The dorsum has a light colored medial stripe from the anterior to posterior bordered by dark patches that are broader between scoli on each side. The flanks have oblique stripes from the dorsal margin of the SD scolus to the posterior of the corresponding D scolus above it (Fig. 6). The 6th instar marks the first appearance of SD2 verrucae, which are partially sunken in the surrounding rough cuticle anterior to the spiracles on A2 to A4. Each is a wart ca. 2× the diameter of the proximal spiracle and has a dense vertical band of tiny spines (Figs. 15–17). In subsequent instars these verrucae are found in the same position on each segment from A2 to A7 (Fig. 17) (see discussion of homology further on); on T1 (Fig. 13), A1 (Fig. 15), and T8 (Fig. 16) they are absent.

The caterpillars feed on one surface of leaf mesophyll in short tracks parallel to the midrib through the 4th or 5th instar (Fig. 4). Later instars feed through the entire leaf except the midrib (Fig. 5). Each instar feeds until about two days before molting, at which time the larva becomes sessile and darkens to a grayish black. Upon molting (Fig. 3), the larva usually eats its cast skin, including the head capsule, before feeding on leaf tissues. In the laboratory the caterpillars were voracious eaters and there were a variable number of larval instars, ranging from 8 to 11 (Table 1). Duration of all larval stages is summarized by the instar that cocooned (Table 2); they are 49 d, 56 d, 63 d, and 73 d for individuals that reached 8th, 9th, 10th, and 11th instars, respectively.

Cocoon: There are more reliable indicators that cocooning (i.e., formation of the cocoon) is imminent than the instar number, which varies from 8 to 11 (Table 2). These include, first, the ventral side (belly) turning orange from its normal pale color and, second, about a day before cocooning, the larva expelling its last fecal pellet



Figures 9–12. Early instars and head of *D. pallivitta* (scanning electron micrographs by S. Kinnee; scale bar = 100 μm). Fig. 9. First instar (D = dorsal tubercle; SD = subdorsal tubercle). Fig. 10. Second instar (note: increase in spines). Fig. 11. Spinneret (spn) and labrum (lbr). Fig. 12. Spinneret, labial (lp) and maxillary (mp) palpi.



Figures 13–18. Selected morphology of 8th instar of *D. pallivitta* (scanning electron micrographs by S. Kinnee; scale bar = 100 μm unless indicated). Fig. 13. Prothoracic spiracle (note: absence of SD2 verruca). Fig. 14. Tarsal claw of thoracic leg (scale bar = 20 μm). Fig. 15. Lateral aspect of thoracic and abdominal segments A1-3; verrucae SD2 on A2 and A3 (scale bar = 1 mm). Fig. 16. Detail of SD2 verruca on A7 (note: A8, right, has no SD2 verruca). Fig. 17. SD2 verrucae on A2 through A7 (scale bar = 1 mm). Fig. 18. Anal proleg with remainder of anal segment (above) and smooth textured ventrum of A9 (below).

Table 2. Duration of larval instar that cocooned for *D. pallivitta*.

Instar that cocooned	N	Mean ± SEM (days)				Adults emerging
		Egg	All larval instars	Cocoon	All stages	
8	12	7.0 ± 0	49.2 ± 2.2	19.1 ± 1.0	75.3 ± 1.9	4♂♂, 8♀♀
9	8	7.0 ± 0	56.6 ± 2.1	18.8 ± 0.9	82.4 ± 2.3	5♂♂, 3♀♀
10	4	7.0 ± 0	63.8 ± 1.3	20.0 ± 0.8	90.8 ± 1.3	1♂♂, 3♀♀
11	1	7.0	73.0	19.0	99.0	1♂♂

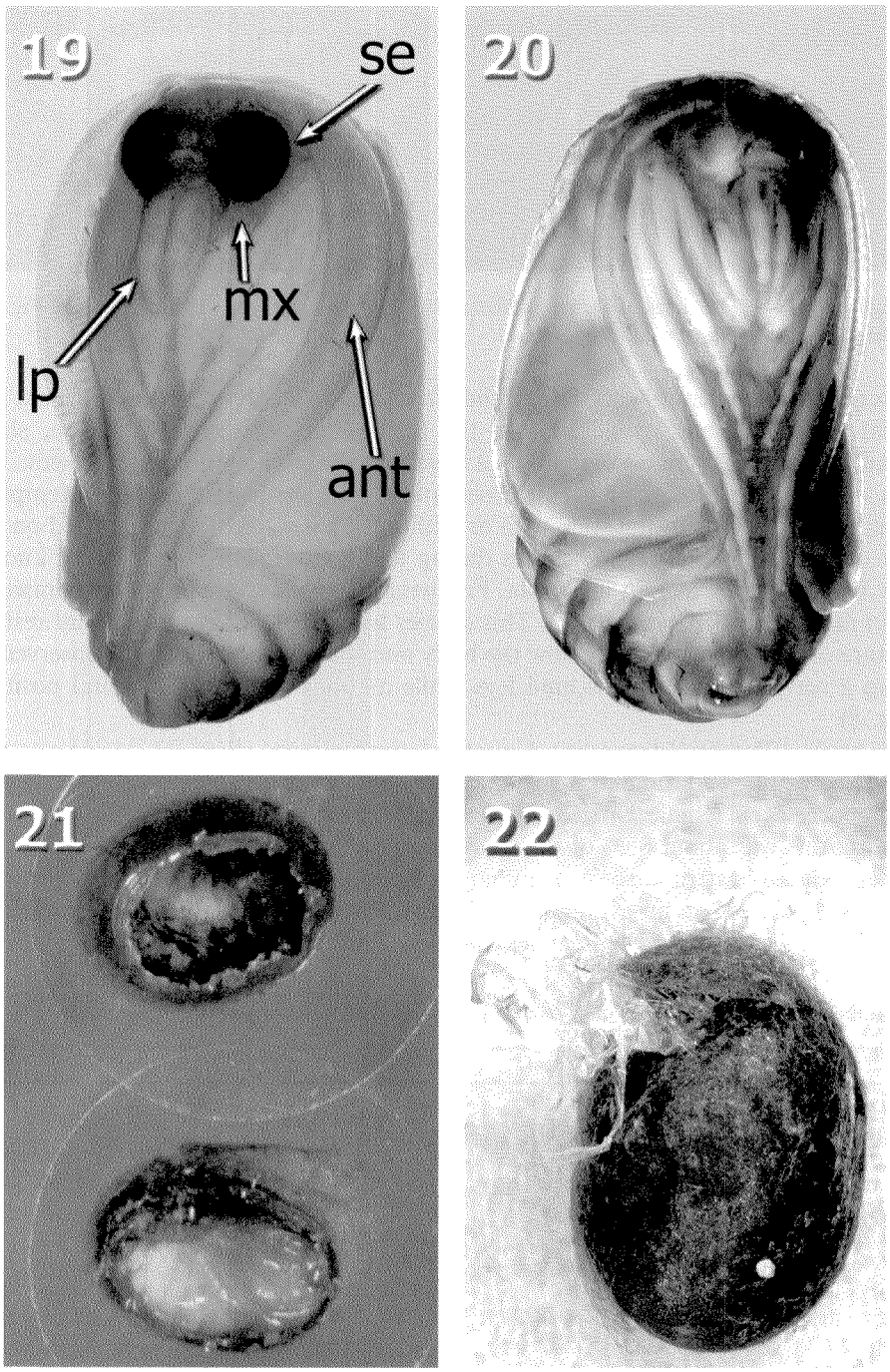
along with a clear, slightly viscous liquid. The prepupa then takes on a "C-shaped" form by wetting itself down, spinning brown silk around itself, and eventually forming a hardened brown outer shell (for a review and description of limacodid cocoon construction see Epstein 1996). The cocoon stage averaged 19 d with a range of 17–21 d. The female cocoon is slightly larger than that of the male (Table 3).

Pupation and duration: Pupation occurs within the cocoon on day 5 after cocooning; the pupa is typical of limacodids in having legs, labial palpi, antennae and wings that are free (Figs. 19–21). The maxillae, which are laterad of the labial palpi are shorter than half the length of these palpi and do not have a lateral extension, which commonly occur in limacodids, although not universally (Epstein 1996). The sculpted portion of the eye is found on the anterolateral margin of the eye, holding the front legs in place between the femoral and tibial junction. Pupae can be most easily sexed by the width of the antenna, which is equal to that of the eye in the basal third (= male) or narrower (= female) (Figs. 19–20). The shriveled larval skin and attached head capsule can be found within the cocoon after adult emergence. The pupa pushes out a cap on one end of the cocoon to emerge (Fig. 22). The duration from egg to adult was 75 d–99 d, depending on the number of larval instars stages (Table 2).

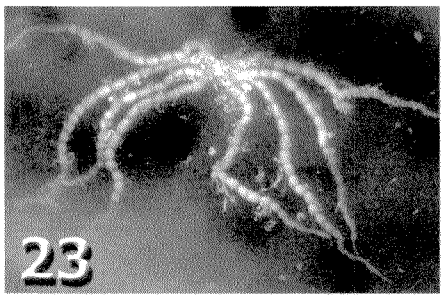
Adult: Adults of both sexes are externally similar except that females are larger, as indicated by forewing length (Table 3), and have filiform rather than bipectinate antennae (Fig. 7) typical of many Limacodidae. The rust-colored forewing is divided by a whitish diagonal line that runs from the midpoint of the inner margin to the

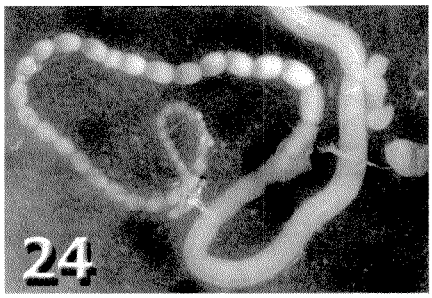
Table 3. Measurements of immature stages and adults of *Darna pallivitta*.

Stage	N	Dimensions (mm)	
		Mean ± SEM	Range
Egg:	10		
Width		1.1 ± 0.07	0.94–1.14
Length		1.6 ± 0.11	1.38–1.74
Cocoon:			
Female - width	11	6.56 ± 0.38	5.81–6.97
- length		8.45 ± 0.54	7.97–9.63
Male - width	14	6.42 ± 0.22	5.98–6.64
- length		7.88 ± 0.31	7.3–8.33
Adult forewing length:			
Female	11	11.89 ± 0.46	10.96–12.45
Male	14	10.51 ± 0.28	9.96–10.96



Figures 19–22. Pupae and cocoons of *D. pallivitta* (images by S. Kinnee unless otherwise indicated). Fig. 19. Male pupa (lp = labial palpus; mx = maxilla; se = sculpted eyepiece; ant = antenna). Fig. 20. Female pupa. Fig. 21. Male cocoons with coverslip windows for pupal observation (prepupa above and pupa below) (photo by W. Nagamine). Fig. 22. Open cocoon with pupal exuvia.





Figures 23–24. Ovarioles of *Darna pallivitta*. Fig. 23. Ovarioles removed from female. Fig. 24. Closeup of developing eggs in ovarioles.

apex (Fig. 7); the ventral surface and the hindwing are a lighter brown. Each sex has labial palpi that are visible beyond the head when viewed from above, short maxillary palpi that are obscured by the labial palpi, and the proboscis is absent. The lack of a proboscis correlates with observations that the female did not attempt to drink from a wetted cotton wick with or without sugar water. Mating started on the first day after emergence, sometimes during the daytime; however it is not known how long the sexes remain in copula. Forewing lengths of both sexes are compared as an indicator of size in Table 3. This species has a typical limacodid adult resting posture of holding the wings below the body and sometimes a moth was observed to grasp a vertical stem with its hind legs while its body hung in horizontal position (Fig. 8).

Fecundity. Potential fecundity: Counts of ovarian eggs (Figs. 23–24) of one-day old females showed potential fecundity to be extremely high (Table 4). Upon emergence, each female carried an average of 573 eggs, and of these, 202 were mature; this was about 35% of the total.

Reproductive attributes: A summary of reproductive attributes is shown in Table 4. Females laid an average of 479 eggs (range = 306–676) over their lifetime, with a hatching rate of 55%. Females can deposit their highest number of eggs on the

Table 4. Reproductive attributes and longevity for ten paired adults of *Darna pallivitta*.

Parameter	Mean ± SEM	Range	Unit
Pre-oviposition period	1.1 ± 0.3	1–2	Days
Oviposition period	6.1 ± 1.0	4–8	Days
Post-oviposition period	2.6 ± 1.5	0–5	Days
Age of first oviposition	2.1 ± 0.3	2–3	Days
Age of peak oviposition	2.1 ± 0.3	2–3	Days
Peak oviposition number	229.3 ± 72.8	124–339	Highest no. eggs laid on one day
Daily oviposition	80.4 ± 20.0	38.2–101	No. eggs laid during oviposition pd.
Total oviposition	479.3 ± 113.4	306–676	No. eggs laid during oviposition pd.
% egg hatch	55.5 ± 18.0	30.4–78.7	No. eggs hatching
Adult ♂♂ longevity	9.7 ± 1.1	8–12	Days
Adult ♀♀ longevity	11.0 ± 1.3	9–12	Days
Potential fecundity (ovarian eggs from ten 1-day old females)			
Mature eggs	201.5 ± 53.5	66–257	No.
Immature eggs	372.0 ± 146.6	110–569	No.
Total eggs	573.5 ± 184.1	176–796	No.

second day after emergence, averaging 229 (range = 124–339). From then on, the number of eggs declined over the six-day oviposition period, while the postoviposition period was 2.6 days. Female and male longevity averaged 9.7 and 11.0 days, respectively.

Discussion

Darna pallivitta has the potential to be a major pest in Hawaii from medical problems resulting from caterpillar stings and from its polyphagous larval feeding habit. The latter is of concern because this species has a high reproductive capacity and invasive status from a limited natural-enemy complex. The average of 479 eggs laid per female is several times higher than other reported pest species of Limacodidae, such as *Latoia viridissima* Holland in Africa (Igbinosa 1992). New generations of caterpillars of *D. pallivitta* are produced rapidly because the female ecloses with 35% of its eggs mature, not needing to feed to lay eggs, while depositing its highest number of eggs on the day after mating. Furthermore, it has continuous generations because there is no diapause (discussed further below). Limacodid caterpillars tend to be generalists on plants with glabrous leaves rather than hostplant specialists (Dyar 1899; Epstein 1996; Wagner 2005; Lill et al. 2006); this enables species such as *D. pallivitta* to feed on a broad array of plants. Although this general strategy as well as larval polyphagy are normal for Limacodidae, *D. pallivitta* appears to have the survival advantages of being the first species of Limacodidae to become established in Hawaii; these include being without the specialized parasitic Hymenoptera and Diptera that normally attack this moth family (see Cock et al. 1987 for information on these parasitoids).

We may now compare the number of instars and duration of larval and pupal stages of *D. pallivitta* with other species of Limacodidae, many of which are considered to be pests. The eleven instars found for some caterpillars of *D. pallivitta* matches the number found for *Parasa* (as *Latoia*) *lepida* (Cramer) (Chayopas 1982), the maximum number known for a species of Limacodidae. Nine instars have been reported for *Phobetron pithecium* (Cramer) (Dyar 1896) and *Acharia hyperoche* (Dognin) (as *Sibine megasomoides* Walker) (Mexzón et al. 1996). Although Dyar (1896) stated that he did not investigate the variability of instars of *P. pithecium*, many other species he reared had seven or eight instars (Dyar & Morton 1896; Dyar 1896; Dyar 1897). While the length of the pupal stage is not known for many limacodids, temperate species appear to remain as prepupae throughout the winter, only pupating a short period before eclosion the following summer (e.g., *Prolimacodes badia* (Hübner))(Wagner 2005; Epstein unpublished). Similarly, several Neotropical species examined by using the cocoon window remained as prepupae for lengthy periods, presumably in diapause to avoid adverse conditions during the dry season (e.g., *Talima postica* Walker)(Epstein unpublished). It is presumed that what is often referred to as "pupal duration" in the limacodid literature is in fact "cocoon duration," since there was no direct observation of the insect inside the cocoon. Therefore, only comparisons of the latter kind can be made between *D. pallivitta* and other limacodid species. The African species *L. viridissima* has a cocoon period of 32.9 days (Igbinosa 1985), suggesting that prepupal diapause did not take place, but this is a longer cocoon period than was found in *D. pallivitta* by nearly two weeks. *Parasa lepida* has a similar cocoon period of 22 days (Desmier de Chenon 1982) to that of *D. pallivitta*. The summer generation of the southern Arizona species of the

related family Dalceridae, *Dalcerides ingenita* (Hy. Edwards), has a similarly short prepupal period to *D. pallivitta* of 3 days (Epstein 1997).

The absence of plant feeding in the 1st instar, as found for *D. pallivitta*, appears to be typical of limacodid species that have caterpillars with spines on scoli or verrucae (e.g., *Euclea* spp., *Acharia* spp., *Parasa* spp., *Natada* spp.) (Dyar & Morton 1896; Dyar 1897). Limacodid caterpillars that become smooth beyond the 1st instar (= gelatine) (e.g., *Apoda*) or retain fleshy tubercles that become hairy and deciduous (e.g., *Phobetron*) begin feeding soon after hatching from the egg (Dyar 1896). Curiously, the first report of nonfeeding 1st instar limacodids was erroneous for *Apoda y-inversa*, a smooth limacodid caterpillar (Dyar & Morton 1895); this, however, was later corrected by Dyar (1898). Dyar's observations on feeding versus nonfeeding 1st instar limacodids have been verified over the last two decades by Epstein (unpublished) and J. Lill (personal communication).

MEE considers the development of nonfeeding 1st instars in spiny limacodids to be related to the tendency for species with spiny caterpillars to lay eggs in overlapping clusters and developmental factors (as discussed further on). This absence of feeding allows these caterpillars to avoid feeding on unhatched embryos in the same egg clusters. Conversely, limacodid caterpillars that feed as 1st instars and become smooth or retain tubercles in later instars hatch from eggs spaced further apart or on different leaves (Dyar & Morton 1895; Dyar 1896). This presumably reduces the probability of unhatched embryos being consumed. Nonfeeding 1st instars can also be viewed to be the result of developmental constraints between spiny caterpillars and their eggs. Unhatched limacodid caterpillars have inverted tubercles or scoli presumably to fit inside the flat egg (Epstein 1996). This is illustrated by the observation that once hatching occurs, the tubercles (Fig. 9) or scoli with 3 to 5 spines evert and the larva greatly expands in height. The shorter time spent as a 1st instar versus the other instars in *D. pallivitta* (2 d vs 5 d or longer) and in other limacodids with spiny caterpillars such as *Parasa lepida* (1 d vs 3.6 d) (Chayopas 1982) suggest that the 2nd instar is nearly developed when the egg hatches. In fact, the short nonfeeding period of 1st instar spiny limacodids can be viewed much like the nonfeeding days that occur prior to molting in the other instars. Furthermore, the 1st instar cuticle before hatching is in essence a covering that protects the flat, ultrathin chorion found in limacodid eggs (Epstein 1996) from the spines of the 2nd instar beneath. The related family Megalopygidae, in contrast, has a feeding spiny 1st instar with a dorsoventrally broad egg roughly the same height and shape of the larva inside, and has a thick chorion (Epstein 1996). This protects the egg from the spiny verrucae beneath and the caterpillar does not need to inflate after hatching.

Limacodid caterpillars are known to be heteromorphic, that is undergoing a change in form from first to later instars (Epstein 1996). *Darna pallivitta* is the first known example of a limacodid caterpillar known to convert elongate 1st instar tubercles into spiny scoli in the 2nd instar. This transformation may be more common than presently known because early instars have been described from only a few Old World taxa such as the spiny *Monema flavescens* Walker (Dyar 1909) and the smooth *Belippa horrida* Walker (Epstein 1996), both from Asia. The elongate 1st instar tubercles of *D. pallivitta* are similar to those in the Holarctic *Apoda* and New World *Phobetron* generic complexes (sensu Epstein 1996). The *Apoda* complex usually has a smooth dorsum after the 1st instar, while the *Phobetron* complex

retains tubercles throughout the larval stage, although they become detachable and hairy. In structure, the tubercles found on *D. pallivitta* are more similar to those of the *Apoda* complex in having a forked apex, whereas in number they match those of *Phobetron* complex in lacking an SD tubercle on the first abdominal segment.

Dyar (1899) referred to limacodid caterpillars with elongate 1st instar tubercles as a "primitive first stage" because they had the most complete setal representation and therefore most primitive known at the time. Dyar's (1899) genealogical tree of limacodid (= eucleid) species occurring in New York State, which is similar to a modern cladogram, has the primitive first stage at the base of the tree, while it is present with some fusion in both the "Palaearctic smooth Eucleids" (= *Apoda* complex) and "Tropic hairy Eucleids" (= *Phobetron* complex), and absent at branch points for the spiny genera termed the "Tropic spined Eucleids" (= *Parasa* and *Natada* complexes) and for the "Tropic smooth Eucleids" (= *Prolimacodes* complex)(all names of generic complexes *sensu* Epstein 1996). First instars of spiny caterpillars of *Parasa* and *Natada* generic complexes typically have three and up to seven spines (in the latter complex) on protuberances that are referred to as scoli rather than tubercles (Epstein 1996). Epstein (1996) followed Dyar's assessment of the 1st instar scoli in the two spiny complexes as being derivative of more simple tubercles; however, he considered those in the *Prolimacodes* complex to be a more primitive type. The setal arrangements found in two African genera, *Pantoctenia* Felder and *Crothaema* Butler, and Asian *Belippa* Walker are now considered to be the most complete and primitive based on homologies of relatively unfused tubercles found in the sister group Dalceridae (Epstein 1996).

Darna pallivitta is also the first known example of a limacodid species with a spiny caterpillar having SD2 verrucae or setal derivative. The only previous report of an unfused SD2 derivative were warts found in 1st instars of smooth caterpillars of African *Crothaema* and *Pantoctenia* (Epstein 1996). At present we do not know whether the SD2 verrucae (Figs. 15–17) occur in other species of *Darna* because examination of images in the literature are inconclusive (e.g., Holloway et al. 1987); the lateral position of the SD1 scoli obscures the spiracles and possible verrucae associated with them. While it is not known whether the phenotypic expression of the SD2 verrucae in later instars of *D. pallivitta* is an anomaly, other examples of developmental shifts of larval characters such as crochets previously reported in Dalceridae (Stehr & McFarland 1985; Epstein 1996) and Limacodidae (Epstein 1996) suggest otherwise for *Darna* and perhaps elsewhere in Limacodidae.

The first attempt to determine the relationship of *Darna* to other limacodid genera was made by Holloway (1986) and Holloway et al. (1987), who placed *Darna* in his "split-back" group. This was the only one of the four assemblages of genera defined by forewing venation rather than by a combination of the type of signum of the female genitalia and the general form of the caterpillar. Future investigation of the caterpillars in the group, both early and late instars, as well as other evidence will be needed to determine whether this grouping is monophyletic. For example, the late instars of two of the "split-back" genera, *Trichogyia* Walker and *Olona* Snellen, have a completely different shape and texture compared to those of *Darna* species (Holloway et al. 1987). However, a close look at the figure of *Olona gateri* West in Holloway et al. (1987) reveals that it has at least three tubercles on each side of a segment, similar to the condition we report here for *D. pallivitta*, except that the tubercles lack spines and are deciduous. Since the early instars of *Olona* are

undescribed, it is not known whether a SD2 row is added beyond the early instars, as occurs in *D. pallivitta*, or is present during the 1st instar as occurs in primitive *Crothaema* and *Pantoctenia* (Epstein 1996).

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